J. Raptor Res. 29(3):187-192

REPRODUCTIVE PERFORMANCE, AGE STRUCTURE, AND NATAL DISPERSAL OF SWAINSON'S HAWKS IN THE BUTTE VALLEY, CALIFORNIA

Brian Woodbridge
USDA Forest Service, Klamath National Forest, 1312 Fairlane Road, Yreka, CA 96097 U.S.A.

Karen K. Finley
31338 S.W. Bellfountain Road, Corvallis, OR 97333 U.S.A.

Peter H. Bloom
Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, CA 93010 U.S.A.

Abstract.—We monitored annual occupancy, reproductive performance, and natal dispersal of a marked population of Swainson's hawks (*Buteo swainsoni*) from 1984–94. Annual territory occupancy varied from 61–90%. Mean annual nest success was 65% (SE = 3.4%), and annual fledging rate was 1.53 (SE = 0.14) young per nest attempt. Of 567 Swainson's hawks banded as nestlings during this study, 41 were later recaptured as breeding adults. Mean age at recapture was 5.9 yr (SE = 0.37; range = 3–15 yr. The mean age of color-marked adults observed in either 1993 or 1994 was 8.2 yr (SE = 0.52), and ranged from 4–15 yr. Dispersal distances from natal site to subsequent breeding site ranged from 0–18.1 km (mean = 8.2 km, SD = 3.1), and was not different from random distances among territories.

Key Words: Buteo swainsoni; *dispersal*; *mark-recapture*; *population demography*; *Swainson's hawk*; *territory occupancy*.

Características reproductivas, estructura de edad y dispersion natal *Buteo swainsoni* en el Butte Valley, California

Resumen.—Desde 1984 a 1994, monitoreamos la ocupación anual, características reproductivas y dispersión natal de una población marcada de *Buteo swainsoni*. La ocupación de territorio varió anualmente desde un 61 a un 90%. La media anual de éxito del nido fue de un 65% (EE = 3.4). La tasa anual de polluelos fue de 1.53 (EE = 0.14) juveniles por nidificación. De 567 individuos marcados como polluelos durante este estudio, 41 fueron recapturados como adultos reproductivos. La edad media de recaptura fue de 5.9 años (EE = 0.37; rango = 3–15 años). La edad media de adultos marcados 1993 o 1994 fue de 8.2 años (EE = 0.52) con un rango de 4 a 15 años. Las distancias de dispersión entre el sitio natal y el posterior sitio reproductivo estaban en el rango de 0 a 18.1 km (media = 8.2 km; EE = 3.1) y no fue diferente a una distancia azarosa entre territorios.

[Traducción de Ivan Lazo]

Declines in numbers of Swainson's hawks (*Buteo swainsoni*) in California (Bloom 1980, Risebrough et al. 1989), Nevada (Oakleaf and Lucas 1976, Herron and Lucas 1978) and Oregon (Littlefield et al. 1984) have stimulated concern over long-term viability of this species' populations in the western United States. Numerous factors have been suggested as causes of regional declines, including loss of nesting habitat (Schlorff and Bloom 1983), conversion of foraging habitat to agriculture (Bloom 1980, Schmutz 1984, Estep 1989), livestock grazing (Littlefield et al. 1984, Woodbridge 1991), predation and interspecific competition (Littlefield et al. 1984, Janes 1987) and environmental contaminants (Henny and Kaiser 1979, Risebrough et al. 1989). Increased mortality during the nonbreeding season, when the bulk of the North American population migrates to South America, has also been suggested as a potential cause of noted declines (Bloom 1980, White et al. 1989).

Neither causes nor remedies for population declines can be addressed without broad understanding of species biology and assessment of long-term patterns in population dynamics. Estimation of demographic parameters allows for analysis of population viability and trends, effects of management actions, identification of critical life history stages, and comparisons with other populations (Noon et al. 1992). Such baseline data have proven essential in conservation of threatened and endangered species (Thomas et al. 1990, Noon et al. 1992).

We describe patterns of territory density, occupancy, productivity, age structure and dispersal in a population of Swainson's hawks over an 11-yr period, and discuss variability in these estimates. This study is part of a long-term investigation of the ecology and demography of Swainson's hawks in northern California.

STUDY AREA

This study took place in the Butte Valley in northern California, approximately 10 km south of the Oregon border and the Klamath Basin. The Butte Valley is included in the Modoc Plateau region of the California sagebrush steppe ecological province (Barbour and Major 1977) and is part of the basin and range physiographic province (Franklin and Dyrness 1973). The study focused primarily on the unforested floor of the Butte Valley, which ranges from 1280–1340 m in elevation and is approximately 415 km^2 in extent. Topography, soils, and natural vegetation of the Butte Valley are typical of the basin and range physiographic province (Franklin and Dyrness 1973). Dominant vegetative associations are western juniper (*Juniperus occidentalis*) woodland (22%), grazed sagebrush steppe (21%), wetlands and seasonally flooded areas (5%), and agricultural fields (53%). Cultivated crops include irrigated alfalfa (*Medicago sativa*), grains, and potatoes.

METHODS

We estimated the size and distribution of the breeding Swainson's hawk population in the Butte Valley by conducting systematic surveys of the valley floor each year from 1983–94. Surveys in the adjacent Klamath Basin consisted of visits to previously known territories. Open, flat terrain and high road densities in agricultural areas permitted good visibility and survey coverage from vehicles. Sage-steppe and juniper woodland habitats were surveyed on foot and from vehicles. In addition to searching for nest sites, we observed any foraging hawk of unknown origin until it returned to a nest site. Survey effort was concentrated during courtship and nest building (mid-April through late May) although new nests were located as late as August.

We defined a territory as an area containing an active nest and defended by a single pair of Swainson's hawks in at least one year. In subsequent years, territories were classified as occupied if at least one adult was observed repeatedly during the early nesting season. A pair was considered to have attempted to breed if a nest was constructed or new material added to an existing nest. Deserted nests were included in the sample if they showed signs of use in the present year (Postupalsky 1974, Steenhof and Kochert 1982). The number of nestlings and unhatched or broken eggs was recorded during at least two nest checks, the first occurring about 1 wk after the mean hatching date (16 June) and the second at banding (4 July to 15 August). We considered a breeding attempt to be successful if ≥ 1 young survived to 5 wk of age. Pairs that built nests but did not breed were included with failed attempts.

To control bias associated with survey timing, lower detectability of failed breeding attempts (Steenhof and Kochert 1982), and to account for permanently abandoned nests discovered in early years of the study, we included only territories which had been occupied at least once during the four previous years in calculations of annual occupancy, nest success, and productivity. The exclusion of newly discovered territories from the annual calculations of annual sucess and productivity may result in a bias toward traditionally occupied territories with older breeders.

We banded nestling Swainson's hawks in the Butte Valley each year from 1980–94. We also marked breeding adults at the nest site by using a mist net with a live great horned owl (*Bubo virginianus*) as a decoy (Hamerstrom 1963, Bloom 1987). Adult hawks were marked with individually numbered plastic legbands and U.S. Fish and Wildlife Service lock-on aluminum bands. Searches for marked individuals were made each year at all known occupied territories, as well as along established transects in foraging habitats. Mean values in the text are presented with standard errors.

RESULTS AND DISCUSSION

Population Size and Density. Swainson's hawks occupying the Butte Valley during the breeding season were almost exclusively territorial adults; we recorded few nonterritorial adult floaters or subadults during the study. The high frequency of marked individuals (80% of breeders in 1994) in the population enabled us to distinguish nonbreeding floaters from territorial pairs and nonterritorial failed breeders.

The number of Swainson's hawk territories monitored during this study increased from 12 in 1984 to 83 in 1994. (Not all of these are included in calculations of reproductive parameters.) Increases during the earlier years of the study were due to improved survey coverage; after 1990, however, fluctuations were related to colonization of new sites and abandonment of traditional territories. Since 1990, 14 new territories were established within the study area, and four traditional territories were abandoned. The dependence of Butte Valley Swainson's hawks on limited high-quality foraging habitats such as sprinkler-irrigated alfalfa was expressed in the locations of newly colonized territories. Twelve of the 14 new territories were established near fields that had recently been converted to alfalfa cultivation.

Table 1. Annual occupancy, nest success, and fledging rate for Swainson's hawk territories in the Butte Valley, California, 1984–94.

YEAR	*N* TERRITORIES[a]	PERCENT OCCUPIED	PERCENT SUCCESSFUL	MEAN NUMBER OF YOUNG FLEDGED PER NEST ATTEMPT (SE)
1984	12		66.7	1.25 (0.37)
1985	13	77	60.0	1.30 (0.40)
1986	22	91	80.0	2.00 (0.26)
1987	34	88	73.3	1.71 (0.23)
1988	38	84	71.9	1.80 (0.20)
1989	45	84	65.8	1.30 (0.20)
1990	56	84	78.7	2.00 (0.20)
1991	64	86	52.7	1.50 (0.20)
1992	66	73	47.9	0.79 (0.14)
1993	64	61	51.3	1.10 (0.15)
1994	73	74	72.2	2.20 (0.15)
Mean		80.2	65.5	1.53
SE		2.8	3.4	0.14

[a] Number of territories sampled.

Most nests were located in western junipers, although four nests were constructed in ponderosa pine (*Pinus ponderosa*), one in an elm (*Ulmus* sp.), two in basin bigsage (*Artemisia tridentata*). Territory distribution was strongly affected by the availability of patches of western juniper in close proximity to agricultural habitats used for foraging (Woodbridge 1991).

Overall territory density was 20/100 km^2. Territory density varied among five large (50–150 km^2) landscape blocks, ranging from 5.7/100 km^2 in irrigated pasture to 36.8/100 km^2 in a landscape dominated by alfalfa cultivation.

Territory Occupancy. The proportion of territories occupied in a given year ranged from 91% in 1986 to 61% in 1993, averaging 80% (SE = 2.8) over all years (Table 1). Fluctuations in annual occupancy rates were caused by non-use of traditional territories and by new pairs attempting to establish territories in previously unoccupied areas. Occupancy also varied among individual territories, ranging from 14–90% of years monitored. At 52 territories with more than five consecutive years of monitoring data, we identified 35 traditional territories that were occupied during most (>50%) years of the study. Seventeen ephemeral territories exhibited low (≤50%) occupancy rates.

Reproductive Success. Between 1984 and 1994 we observed 454 nest attempts. Overall, pairs were successful in 65% (SE = 3.6) of reproductive attempts, with annual success ranging from 48–80% (Table 1). Success rates were significantly lower during the period from 1991–93. Nesting failure between 1986 and 1990 typically resulted from loss of nestlings (51% of failures), failure to lay eggs (24%), failed incubation (17%) and incomplete nest-building (8%; Woodbridge 1991). Known nestling losses that resulted in nest failure were caused by starvation ($N = 21$), predation by great horned owls ($N = 5$) or golden eagles (*Aquila chrysaetos*) ($N = 2$), windstorms ($N = 5$) and human disturbance ($N = 3$).

Fledging Rate. The mean fledging rate for all nest attempts was 1.53 (SE = 0.14) young per nest attempt, ranging from 0.79 (SE= 0.14) in 1992 to 2.20 (SE = 0.15) in 1994 (Table 1). Mean annual fledging rates varied among individual territories. Of 52 territories with more than five consecutive years of monitoring data, 11% exhibited low (<0.5 young/attempt) fledging rates; an additional 11% fledged <1.0 young/attempt. Fledging rates were >1.50 young/attempt at 42% of monitored territories. Territories with consistently low reproduction were associated with sage-steppe habitats, whereas agricultural habitats supported higher reproductive rates (Woodbridge 1991).

Mark-recapture Results. We banded 567 nestling Swainson's hawks in the Butte Valley between 1979 and 1994. Forty-one of these marked nestlings were recaptured as breeding adults in subsequent years, and nine were recovered as post-fledging mortalities within the Butte Valley. An additional eight were recovered in Latin America, giving an overall band return rate of 10.2%. The virtual absence of subadult Swainson's hawks in the study area, however, suggests that these birds spend their second summer elsewhere, and may not be available for recapture. This would result in underestimation of band return rates, which are largely based on recapture of breeding adults.

Population Age Structure. Swainson's hawks occupying the Butte Valley during the breeding season were almost exclusively in adult plumage; we recorded only 12 individuals in subadult plumage. Subadults observed early in the season (April to May) were typically absent after mid-May, and were assumed to be late migrants. Paired territorial Swainson's hawks in subadult plumage were re-

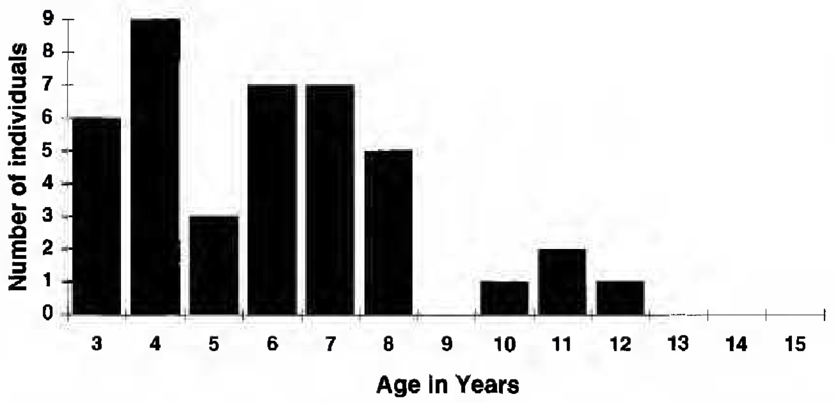

Figure 1. Frequency distribution of age at recapture of 41 Swainson's hawks banded as nestlings in the Butte Valley, California, 1980–94.

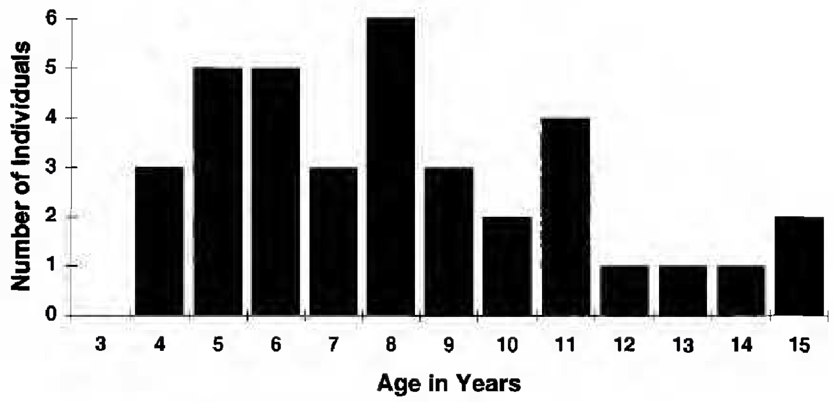

Figure 2. Frequency distribution of ages for 36 Swainson's hawks banded as nestlings in the Butte Valley, California (1980–92) and observed in 1993–94.

corded on four occasions; in all cases the subadult hawk was female. One subadult male acted as a nest helper, provisioning young at a nest also tended by an adult pair.

Forty-one Swainson's hawks banded as nestlings in the Butte Valley have been recaptured as breeders since 1981. The mean age at recapture was 5.9 yr (SE = 0.37), ranging from 3–12 yr (Fig. 1). Age at recapture should not be interpreted as age of first breeding; many of these individuals may have bred elsewhere or eluded capture for several years before recapture. Of five 3-yr-old Swainson's hawks recaptured as territorial breeders (assumed first breeding), two were still in subadult plumage, suggesting some variability in maturation rates.

Approximately 80% of the 41 recaptured and color-marked Swainson's hawks were observed at least once in subsequent years. The age distribution of color-marked birds observed in either 1993 or 1994 (N = 36) ranged from 4–15 yr, with a mean age of 8.2 yr (SE = 0.52; Fig. 2). We believe that this is our best estimate of the age distribution of the breeding population. Mortalities of known-age Swainson's hawks were caused by collision with a train (one 6-yr-old male) and probable collision with vehicle (one 15-yr-old male).

Dispersal. We used natal dispersal distances and interterritory movements of marked adult Swainson's hawks to assess immigration and emigration in this study area. For 41 nestlings recaptured as breeding adults (20 female, 21 male), dispersal distances ranged from 0–18.1 km, and averaged 8.8 km (SE = 1.1 km). Mean distance between natal and subsequent breeding sites was not statistically different from random interterritory distance (t = 1.06, P = 0.17, two-tailed), and did not differ between sexes (t = 1.33, P = 0.12, two-tailed). Our estimate of dispersal distance may be biased low, since survey effort is not as extensive in the adjacent Klamath Basin. Two breeding adults recaptured in the Butte Valley had moved 10.2 km and 7.9 km from natal sites in the adjacent Klamath Basin. We recorded only one confirmed case of natal dispersal to a breeding territory outside of the Butte Valley; this bird was found breeding at a territory in the Klamath Basin, 36.8 km from its natal site. A nestling banded in 1982 was found injured in April 1988 in Diamond Valley, Nevada, 565 km southeast from its natal site. Another nestling banded in 1979 was found injured in August 1981, in Christmas Valley, Oregon, 160 km northeast of its natal site. Whether these hawks were breeding at their recovery sites is unknown.

Dispersal of hawks into the Butte Valley from natal sites in the Klamath Basin suggests that the Butte Valley is not a closed population, and there may be substantial genetic interchange with the Klamath Basin area. The two areas are likely interacting elements of one metapopulation. Territory occupancy and reproductive success, however, differed dramatically between the two areas during the same period. Bloom and Hawks (in Risebrough et al. 1989) reported $<50\%$ territory occupancy and $<50\%$ nest success in the Klamath Basin in the mid-1980s, considerably less than in the Butte Valley. Because of unequal levels of marking and monitoring in the two areas, we were unable to quantify the level of exchange.

Within the Butte Valley study area, we recorded 25 interterritory movements by marked adult Swainson's hawks (11 male, 14 female). These movements ranged from 0.97–6.3 km (mean = 2.2, SE = 0.23 km), and typically were short moves between neighboring territories. Mean adult dispersal distance was significantly less than the mean nearest-neighbor distance (3.7 km, SE = 0.87) for the Butte Valley population ($t = 6.77$, $P = 0.03$, one-tailed). Of 36 adult hawks marked in the adjacent Klamath Basin between 1981 and 1988, none were observed within the Butte Valley.

While evidence of natal dispersal and individual movements to and from our study area are valuable preliminary data, assessments of immigration and emigration would be greatly enhanced by more comprehensive monitoring of breeding Swainson's hawks in the neighboring Klamath Basin. Among other things, this would help us assess the extent to which the Butte Valley serves as a source population for more marginal habitat areas to the north and east.

Concluding Remarks. Because Swainson's hawks are long-lived, description of population demography requires long-term study of marked populations in order to account for the effects of generation time and environmental variability (Newton 1979, Noon et al. 1992). Temporal variability in reproductive performance such as we have observed during the course of this study may or may not translate into long-term changes in the local Swainson's hawk population. Assessment of critical values may best be accomplished through mathematical modelling of population trends based on life history matrices.

Identification of conservation measures for maintaining the long-term viability of this population depends on analysis of the extent to which differences in reproductive success and nestling survival are habitat related. The presence of both traditional and marginal ephemeral territories in our study area suggested that a subset of territories contributed disproportionately to the long-term viability of the population. In our area, cultivated alfalfa appears to have become a critical habitat element (see Woodbridge 1991), replacing the productive native grasslands which were the original vegetation. Conservation measures that restore productive perennial grasslands and open shrubsteppe habitats on public lands and Conservation Reserve lands in the Butte Valley might ensure the resilience of Swainson's hawks to changes in agricultural ecomomics and practices.

ACKNOWLEDGMENTS

We owe thanks to the many field technicians and student interns who contributed to this project over the years. C. Cheyne, S. Baker, J. Montejo Diaz, A. Strassler and T. Seager in particular were instumental to the success of this project. T. Farmer and J. Stout of the Goosenest Ranger District, Klamath National Forest, provided financial and logistical support for our studies in the Butte Valley. The assistance and camaraderie of S. Hawks, B. Clark, E. and J. Henckel and S. Bales in collection of Klamath Basin data is gratefully acknowledged. Partial funding was provided by Brian Walton of the Predatory Bird Research Group.

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Received 20 January 1995; accepted 22 May 1995